Review of Palaeobotany and Palynology 249 (2018) 16–23

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

An early Oligocene occurrence of the palaeoendemic genus *Dipteronia* (Sapindaceae) from Southwest China

Wen-Na Ding [a,b], Jian Huang [a,b], Tao Su [a], Yao-Wu Xing [a,*], Zhe-Kun Zhou [a,c,**]

[a] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] Key Laboratory of Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China

ARTICLE INFO

Article history:
Received 6 May 2017
Received in revised form 5 November 2017
Accepted 7 November 2017
Available online 20 November 2017

Keywords:
Biodiversity
China
Climate change
Dipteronia
Fossil history
Rupelian

ABSTRACT

Palaeoendemic plants, whose past geographical distribution was much larger than their present distribution ranges, play an important role in reconstructing biogeographical events, and in tracking floristic relationships among continents throughout geological time. Improving knowledge about their geographical histories helps to understand the evolution of biodiversity under palaeoenvironmental changes. Here, we report the first fossil record of *Dipteronia* from East Asia, namely *Dipteronia brownii* McClain et Manchester, based on diagnostic winged fruit remains from the Rupelian (c. 32 ± 1 Ma) of the Lühe Basin in southwestern China. The fossil species is characterized by (i) a samaroid mericarp, with an orbicular wing, (ii) a primary vein extending from the attachment scar, and ramifying into secondary and tertiary veins that radiate out from the seed body area and dichotomize toward the mericarp. *Dipteronia* was widely distributed in the Northern Hemisphere during the Palaeogene and is now endemic to central and southwestern China with two extant species. This new finding significantly expands the historical distribution of *Dipteronia* into China by the early Oligocene, and its present-day endemism is apparently the result of extirpation from North America and the higher latitudes of Asia associated with Cenozoic climatic changes.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Palaeoendemics are geographically restricted ancient taxa, that often suggest that they have been selected against in other regions (López-Pujol et al., 2011; Jordan et al., 2015). Recently diversified taxa that did not have enough time to disperse broadly are classified as neoendemics (Manchester et al., 2009; López-Pujol et al., 2011). The majority of Chinese neoendemics is distributed in the southeastern and eastern edges of the Tibetan Plateau (Hengduan Mountains sensu lato), where adaptive radiations were triggered by the recent (late Neogene) uplift of the Hengduan Mountains (Liu and Tian, 2007; Favre et al., 2015; Xing and Ree, 2017) and the resulting allopatric speciation and habitat fragmentation across elevational ranges. In contrast to the situation for neoendemics, most palaeoendemics have been found scattered within the relatively low latitudes of mountainous enclaves in central (mainly Mounts Qinling and Daba), southern (Mounts Nanling and Yunkai) and eastern China (e.g., Mount Tianmu) (Manchester et al., 2009; Huang et al., 2011; López-Pujol et al., 2011; Huang et al., 2012; Huang et al., 2015; Huang et al., 2016a). These regions are characterized by relative tectonic stability since the Neogene (Hsu, 1983).

East Asia is well-known for its high plant diversity and abundant palaeoendemics (Zhou and Momohara, 2005; Manchester et al., 2009). Previous studies have found that many palaeoendemic genera currently present in East Asia, occurred widely in North America and/or Europe (Wen, 1999; Milne and Abbott, 2002; Manchester et al., 2009), and their distribution patterns have been significantly influenced by Cenozoic climatic changes (Milne and Abbott, 2002; Feng et al., 2015). Disentangling their biogeographic histories will help to understand the evolution of biodiversity under palaeoenvironmental changes (Ferguson et al., 1997; Kreft and Jetz, 2013; Zhang et al., 2016). Despite increasing interest in the timing and development of biodiversity between continents (Wood, 1972; Wolfe, 1978, 1980; Hsu, 1983; Tiffney, 1985; Manos and Donoghue, 2001; Weber, 2003; Manchester et al., 2009; Huang et al., 2016b), the poor fossil record of endemics within East Asia has limited our understanding of the evolution of biodiversity and floristic relationships among different regions.

Dipteronia (Sapindaceae) is an ancient relictual woody genus in East Asia and is endemic to southern and central China with two extant species: *Dipteronia sinensis* and *Dipteronia dyeriana*. *Dipteronia sinensis* has a relatively wide distribution in central China (Gansu, N Guizhou, SW Henan, W Hubei, Hunan, Shaanxi, S Shanxi, and E Sichuan), whereas *D. dyeriana* is restricted to small isolated areas in southeastern Yunnan

* Corresponding author.
** Correspondence to: Z.K. Zhou, Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China.
E-mail addresses: ywxing@xtbg.org.cn (Y.-W. Xing), zhouzk@xtbg.ac.cn (Z.-K. Zhou).

https://doi.org/10.1016/j.revpalbo.2017.11.002
0034-6667/© 2017 Elsevier B.V. All rights reserved.

(Xu et al., 2008a; Fang et al., 2011). Both species occur naturally in mixed forest margins at altitudes ranging from 1000 to 2500 m, characterized by fog in winter and spring (Ouyang et al., 2007; Xu et al., 2008a; Zhang et al., 2014). Compared to its modern restricted distribution, *Dipteronia* was present in the Far East and North America during the Palaeogene (McClain and Manchester, 2001), where they disappeared by the end of the Oligocene according to fossil records (McClain and Manchester, 2001). However, when *Dipteronia* migrated to China and where it came from were still unknown due to the lacking fossil record. Here, we present a newly discovered fossil occurrence of *Dipteronia* fruits from the early Oligocene of Yunnan, southwestern China. The fossil fruits have been studied morphologically and are compared with both extant and fossil representatives of *Dipteronia*. We discuss the implications of this discovery for documenting the origin of palaeoendemic taxa and understanding floristic changes between East Asia and North America in the Cenozoic.

2. Material and methods

2.1. Geological setting

Two winged fruits of *Dipteronia* were found as impressions in lacustrine mudstones at the locality where fossil dicotyledonous leaves are the most abundant. The fossil site is situated near Lühe Town, Chuxiong Yi Autonomous Prefecture, Yunnan Province, P.R. China (25°8.5′N, 101°22.5′E, 1, 882 m a.s.l.; Fig. 1). The lacustrine sediments of the study site are characterized by laminated yellow and dark grey silty mudstones, with several layers of coal and volcanic ash. Recent U–Pb zircon dating of the three lowermost volcanic ash layers yielded a rather distinct age, uniformly c. 32 ± 1 Ma (Linnemann et al., 2018). These dates are generally interpreted as being the age of deposition for the fossil-bearing strata of the Lühe site in the Rupelian stage of the Oligocene.

The Oligocene fossiliferous lacustrine deposits, superimposed on Cretaceous purple-red silty mudstones, are overlain by Quaternary laterites (Zhang, 1996). The lacustrine section is partly lithostratigraphically correlated with the lignite-bearing section exposed in the nearby Lühe Coal Mine (Zhang, 1996; Xu et al., 2008b). The mine section has yielded plant remains, including woods (Yi et al., 2003), *Sequoia* (Ma et al., 2005), *Equisetum* (Zhang et al., 2007), as well as a rich palynoflora (Xu et al., 2008b), which is regarded as late Miocene flora based on the geological survey and coeval floristic similarities (Zhang, 1996; Xu et al., 2008b). The dating age of the lacustrine deposits in Lühe Town is also the minimum age of zircon populations in fluvial units within the mine as reported by Wissink et al. (2016), and supports the correlation between the Lühe Town section and that exposed in the nearby mine.

The fossils of *Dipteronia* were collected along with other winged fruits such as *Acer*, *Ailanthus*, *Fraxinus*, *Ostrya*, *Palaeocarya*, and *Carpinus* from the upper part of the Oligocene lacustrine deposits, which are composed of laminated greyish-yellow mudstones with numerous remarkable fossil impressions (Fig. 2). Besides fruits, this layer yielded abundant leaf fossil gymnosperms, e.g., *Cryptomeria* (Ding et al., 2017), *Metasequoia*, *Sequoia*, and angiosperms, e.g., *Acer*, *Carpinus*, *Castanopsis*, *Mahonia*, *Ostrya*, *Populus*, *Quercus*, as well as fishes.

2.2. Methods

Photos were taken using a Nikon D700 digital camera. Detailed structures of these specimens were observed and photographed using a Leica S8AP0 stereo microscope.

Dipteronia fruits were described following the terminology of McClain and Manchester (2001). Fruit length was measured along the longest line parallel to the primary vein approaching the seed. Fruit width is the longest line perpendicular to its length. The diameter of the seed is the line parallel to the primary vein. The length of the attachment scar is shown as a prominent vascular trace extending from the apical end of the fruit before deflecting to the centrally positioned seed.

Morphological measurements were made using Image J Version 1.47 (http://rsb.info.nih.gov.ig/). Line-drawings of the fossil specimens were created using CorelDraw X7 (Corel, Ottawa, Canada). The geographic distributions of extant and fossil occurrences of *Dipteronia* (Fig. 3) were plotted using ArcGIS 9.3 software (ESRI, USA) by entering latitudes

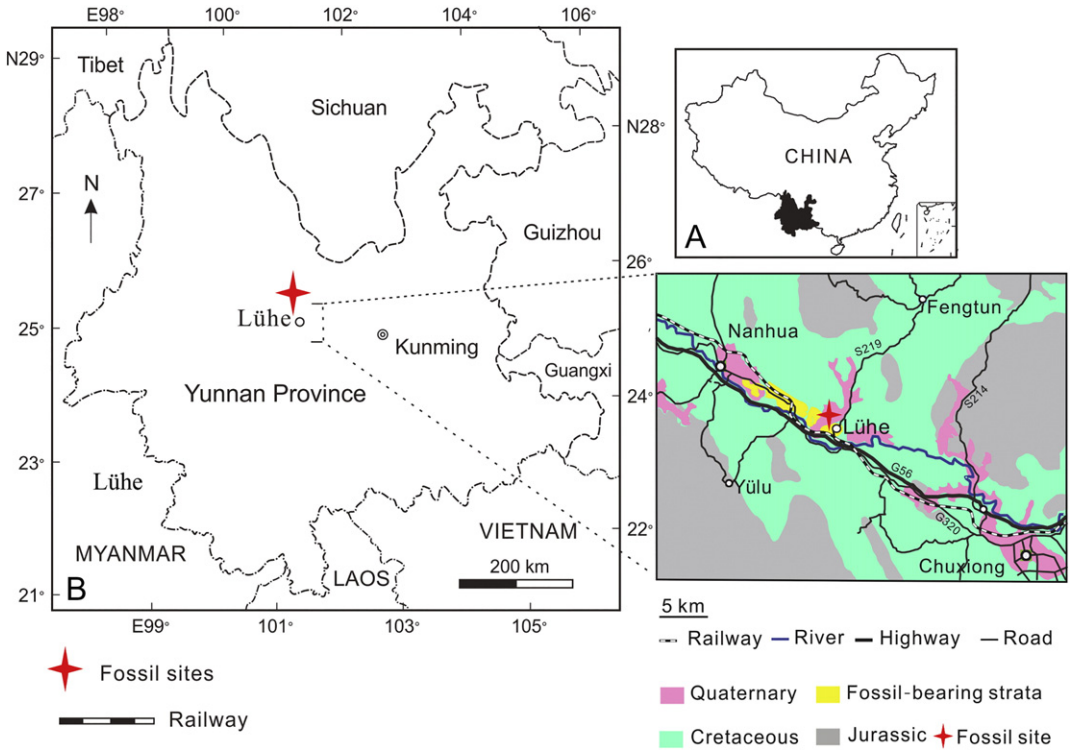

Fig. 1. The Lühe fossil locality from which *Dipteronia* was collected in central Yunnan, SW China.

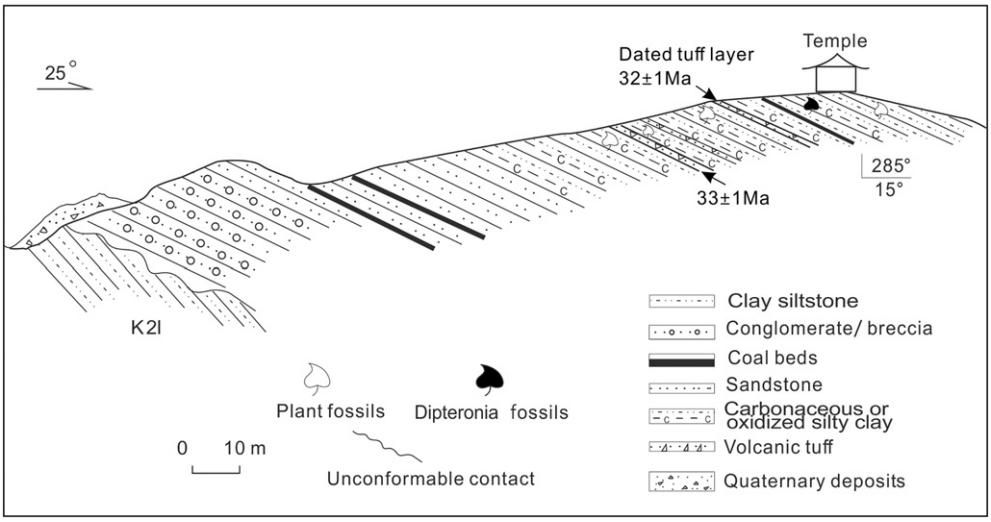

Fig. 2. Geological cross section of the outcrop in Lühe Town, central Yunnan, SW China.

and longitudes of sites. The geographic coordinates and stratigraphic position of localities from which *Dipteronia* fossil fruits have been collected were taken from previous publications (McClain and Manchester, 2001; Manchester et al., 2009). Climatic data for modern distribution ranges of *Dipteronia* were extracted from Fang et al. (2011). Fossils were compared with extant specimens of *Dipteronia dyeriana* cultivated from Kunming Institute of Botany and *Dipteronia sinensis* from the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

3. Results

3.1. Systematics

Family: SAPINDACEAE Jussieu, 1789.

Genus: ***Dipteronia*** Oliver, 1898, 1889.

Species: *Dipteronia brownii* McClain et Manchester, 2001.

Previous nomenclature:

1935 *Dipteronia americana* Brown, pp. 580, pl. 67, figs. 6, 12.

1937 *Dipteronia insignis* (Lesquereux) Brown, pp.181, pl. 59, figs. 10–12.

1987 *Bohlenia americana* (Brown) Wolfe et Wehr, pp.19, pl. 13, figs. 1–8.

1987 *Bohlenia insignis* (Lesquereux) Wolfe et Wehr, pp. 23.

1999 *Dipteronia insignis* (Lesquereux) Brown, pp. 492–493, fig. 10b.

2001 *Dipteronia brownii* McClain et Manchester, pp. 88, figs. 10–34.

2009 *Dipteronia brownii* McClain et Manchester, pp. 26–28, fig. 40.

Specimens checked: Two fruits are impressions, specimen numbers are KUN PCLH1-0425 (Plate I, 1–5), and KUN PCLH1-0074 (Plate I, 6–8).

Locality: Lühe Town, Nanhua County, Yunnan Province, China (Fig. 1).

Age: Rupelian (c. 32 ± 1 Ma).

Repository: The Herbarium of Kunming Institute of Botany (KUN), Chinese Academy of Sciences.

3.2. Description

Fruits seemly schizocarpic, with a single suborbicular, samaroid mericarp (Plate I, 1–8). Mericarp with a central flattened round to pyriform endocarp, 4.7–5.1 mm in diameter, surrounded by a flat, suborbicular 21 mm long and 17 mm wide wing, with a length to width ratio of 1.2. Wing margin entire, rounded, except for a flat attachment scar on the proximal edge (Plate I, 1, 2). Primary vein extending from the end of the attachment scar, 3 mm to the apical end of the attachment scar, then deflecting sharply at 130° and extending straight 3.6–6.0 mm to the centrally positioned seed of each mericarp (Plate I, 1, 2). Secondary veins forming a reticulum over the endocarp (Plate I, 2). Tertiary veins radiating out from the seed body, dichotomizing and vascularizing to the wing margin (Plate I, 5, 7, 8). Quaternary veins forming a fine reticulum of polygonal areoles throughout the wing with few or no free-ending veinlets (Plate I, 5, 8).

4. Discussion

4.1. Comparison with fossils and extant species of Dipteronia

Fossil records of *Dipteronia* are rare, and their distribution was previously assumed to have been restricted to the Palaeogene in North America (McClain and Manchester, 2001) and the Far East (Akhmetiev et al., 2002). All fruit fossils of *Dipteronia* from North America were examined and assigned to a single species, namely *Dipteronia brownii* McClain et Manchester (McClain and Manchester, 2001); *Dipteronia* fossil fruits from southeastern Russia were only assigned to generic level due to the limited number of morphological characters preserved (Manchester et al., 2009).

Fossil mericarps of *Dipteronia brownii* from western North America range from 8 to 24 mm in diameter, and pericarps range from 3 to 8 mm in diameter (McClain and Manchester, 2001). Our fossils fall within the range of variation in size and shape. Even though our fossils have a shallow concavity in the wing on the basal side adjacent to the attachment scar (Plate I, 1, 2), no distinctive morphological differences can be observed in the North American fossils. The fruits of *D. brownii* are comprised of two to three mericarps (McClain and Manchester, 2001), whereas the winged fruits of our fossils are detached, showing only isolated mericarps. Nonetheless, the attachment scar indicates that our fossil shared two or more mericarps (Plate I, 1), instead of developing only one mericarp with another abortive one, as it can occur in the living species (Plate II, 2, 6). Because the mature schizocarps were joined at the proximal edge, mericarps split apart evenly along the median axis, typically leaving a flat proximal attachment scar on each mericarp; if the schizocarp was composed of one abortive mericarp and another mature mericarp (Plate II, 2, 6), the abortive one would be protruded or split up unevenly with the matured mericarp at the apical end of the attachment scar.

Modern *Dipteronia* fruits have distinctive winged schizocarps typically composed of two orbicular or obovate mericarps. Sometimes they develop one mature mericarp while the other is abortive (Plate II, 2, 6). The two extant species of *Dipteronia* differ in overall size and the

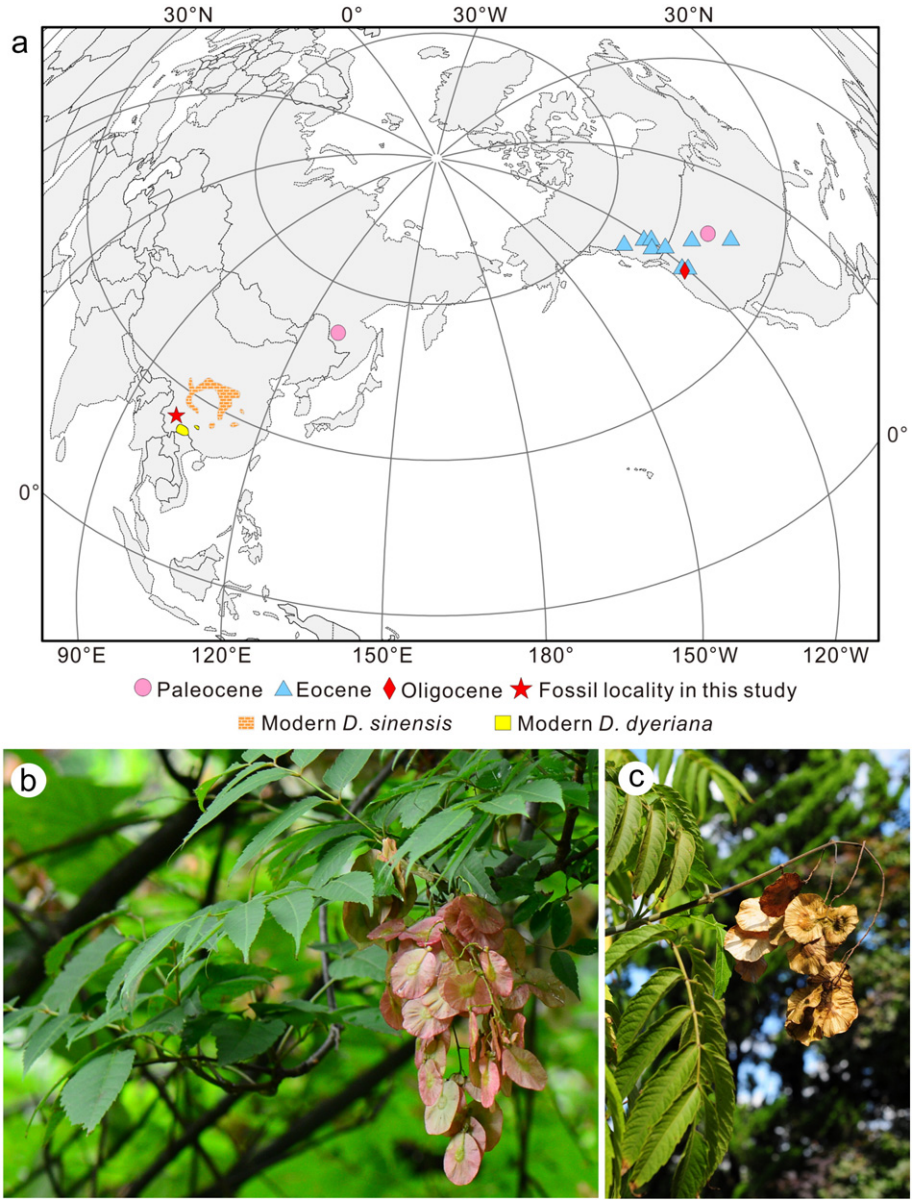

Fig. 3. Modern distribution ranges and fossil records of *Dipteronia* (a), and fruiting branches of the living species of *Dipteronia* (b. *D. sinensis*, c. *D. dyeriana*).

thickness of the pericarp around the seed (Plate II, 5). Mericarps of *Dipteronia dyeriana* are thicker than *Dipteronia sinensis*, and the size of mericarps in *D. dyeriana* is ca. 4.5–6.0 cm in diameter, which is significantly larger than *D. sinensis* (ca. 2.1–2.4 cm). Fruits of *Dipteronia brownii* from Lühe were smaller than those of *D. dyeriana* but had approximately the same range of variation in shape and size as *D. sinensis*. However, the ratio of attachment scar to the main body of the mericarp in our fossils (0.18) is significantly larger than *D. sinensis* (0.29) but close to *D. dyeriana* (0.19).

As discussed above, our fossils show combined characteristics of *Dipteronia sinensis* and *Dipteronia brownii* and fall within the range of morphological variability of *D. brownii*. Therefore, we adopt a broad circumscription and assign our fossils to *D. brownii*.

4.2. Implications for biogeography and the origin of palaeoendemics

Currently, *Dipteronia* is allopatrically distributed in central and southwestern China, occurring in humid mountainous regions at altitudes from 1000 to 2500 m with fog in winter and spring seasons (Ouyang et al., 2007; Zhang et al., 2014). Compared to its current limited distribution, *Dipteronia* had a much wider distribution in the Northern Hemisphere including North America, the Far East and East Asia, but not in Europe throughout the Cenozoic (Fig. 3, Table 1). The earliest known *Dipteronia* fruits were of Palaeocene, from Fort Union Formation of Hell's Half Acre, central Wyoming, western North America and Tsagayan Formation of Amur region, southeastern Russia (McClain and Manchester, 2001; Akhmetiev et al., 2002; Manchester et al., 2009). Subsequently, *Dipteronia* fruit fossils occurred in North America from the middle Eocene to the early Oligocene (Meyer and Manchester, 1997; McClain and Manchester, 2001; Manchester et al., 2009) and in southwestern China in the Rupelian. The specimens from Lühe represent the southernmost fossil record of *Dipteronia*, and expand the occurrence of this genus to China to the early Oligocene. Based on the fossil record, *Dipteronia* exhibits an East Asia–North America disjunction pattern during the Palaeogene. The spread of taxa around the Northern Hemisphere has been facilitated intercontinentally by two major migration routes, the Bering and North Atlantic land bridges (Tiffney, 1985; Xiang et al., 1998; Manchester, 1999; Wen, 1999, 2001; Manos and Donoghue, 2001; Milne, 2006; Wen et al., 2016). As no *Dipteronia* fossils have been found in Europe, we conclude that this

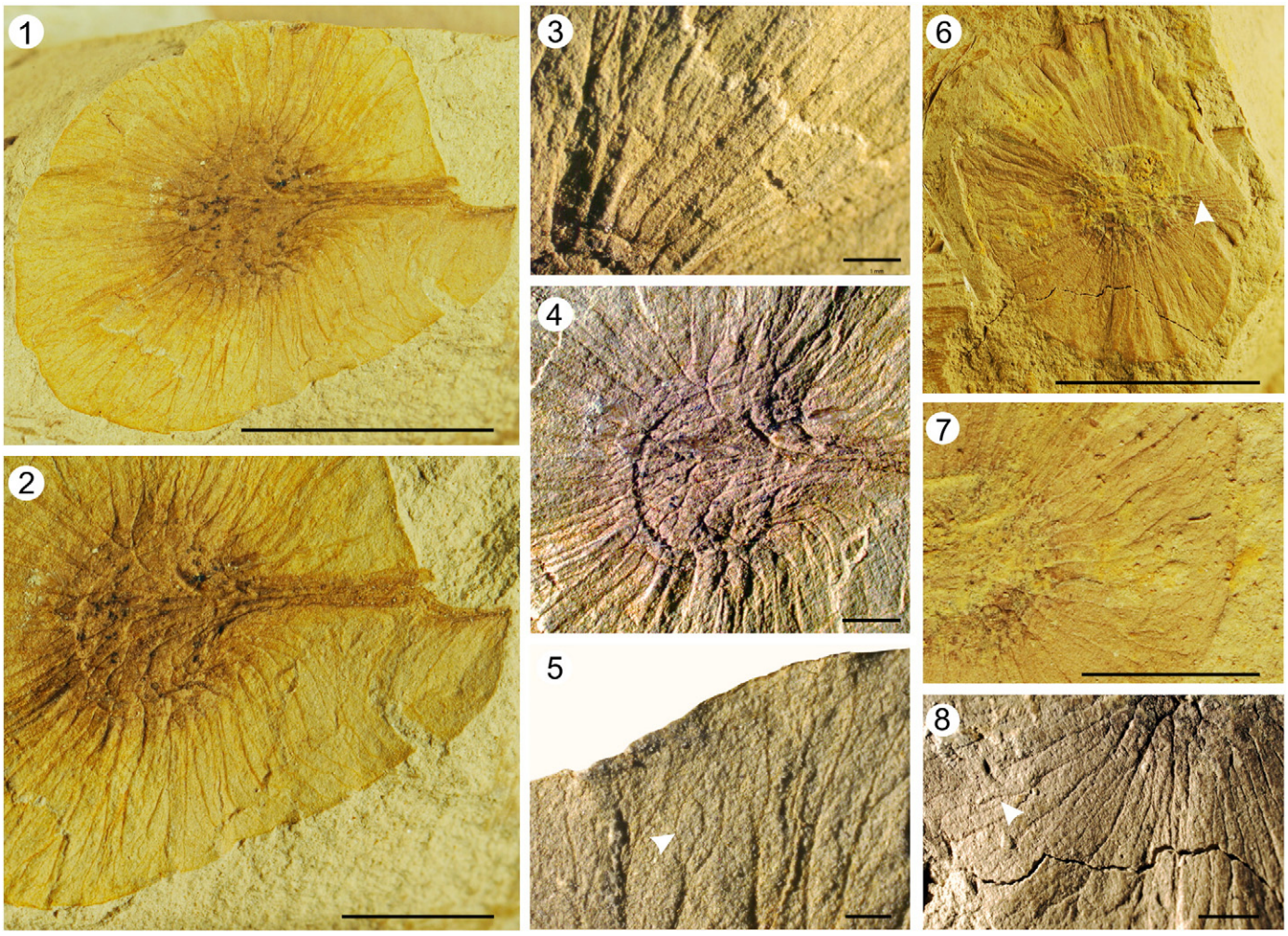

Plate I. *Dipteronia brownii* McClain et Manchester impression fossils from the Rupelian Lühe flora of Yunnan. 1–5. KUN PCLH1-0425. 1. General view of the mericarp. Scale bar = 1 cm. 2. Enlargement of the multistranded primary vein. Scale bar = 5 mm. 3. Showing radiating veins near the margin of the pericarp. Scale bar = 1 mm. 4. Dichotomizing secondary and tertiary veins over the mericarp, and the margin of the seed body. Scale bar = 5 mm. 5. Showing the reticulum of the tertiary veins (arrow) near the margin. Scale bar = 0.5 mm. 6–8. KUN PCLH1-0074. 6. General view of the mericarp, the arrow showing the primary vein giving rise to dichotomizing secondary veins. Scale bar = 1 cm. 7. Showing the dichotomizing secondary and tertiary veins. Scale bar = 5 mm. 8. (arrow) near the margin of the mericarp. Scale bar = 1 mm.

genus might migrate between North America and East Asia via the Bering land bridge by the Palaeogene when the climate was warmer and the land bridge was present (Tiffney, 1985; McClain and Manchester, 2001; Milne, 2006; Wen et al., 2016).

Dipteronia became extinct in North America by the end of the Oligocene (McClain and Manchester, 2001). Likewise, several other coeval taxa disappeared from North America before the end of the Oligocene, such as *Craigia*, *Davidia*, *Euptelea* and *Hovenia* (Manchester et al., 2009; Xing et al., 2016). These palaeoendemics are likely to be geographically restricted due to climatic changes rather than dispersal limitation, because the main migration routes, the Bering land bridge and the North Atlantic land bridge, were still available for long-distance dispersal during the Palaeogene (Marincovich and Gladenkov, 1999; Milne and Abbott, 2002). Therefore, the establishment of palaeoendemics might have been correlated not only with land bridge severance and the emergence of barriers to dispersal but also with the ability of plants to adapt to climate change. There was a general trend toward a cooler and drier climate since the Oligocene in the high latitudes of the Northern Hemisphere (Ivany et al., 2000; Zanazzi et al., 2007; Eldrett et al., 2009; Liu et al., 2009; Xiao et al., 2010; Lielke et al., 2012; Sun et al., 2014; Lu, 2015). Genera that were able to adapt to the deteriorating climatic conditions survived, whereas genera such as *Dipteronia* became extinct in North America but survived in the refugial areas of East Asia (Tiffney and Manchester, 2001; Zhou and Momohara, 2005; Manchester et al., 2009). Even though the origin of palaeoendemics in East Asia is still quite uncertain because of the incomplete fossil record, especially from the Palaeogene, the present fossils of *Dipteronia* provide hard evidence that this genus already occurred in China by the Rupelian, and its present-day endemism might be the result of regional extinctions in North America and the Far East during the Cenozoic (Xing et al., 2016).

Endemic groups represent important elements in defining floristic regions, and understanding their biogeographic histories is crucial to infer the evolution of certain floras (Zhou and Momohara, 2005). Several authors proposed that most endemism arose in the late Pliocene to early Pleistocene due to local extinction under climate change (Hewitt, 2000; Willis and Niklas, 2004; Su et al., 2013; Favre et al., 2015) and tectonic events (Wen, 1999; Milne and Abbott, 2002; Zhou and Momohara, 2005; Wu et al., 2007; Manchester et al., 2009). However, the fossil history of *Dipteronia* suggests that this genus became endemic to China as early as the Oligocene which is much older than previous thought (Milne and Abbott, 2002; Zhou and Momohara, 2005; Manchester et al., 2009; Wu et al., 2007; Zhou, 2013).

As discussed above, *Dipteronia* fruit fossils fall within the range of variation in general size and shape of *Dipteronia sinensis*, which demonstrates that the genus has retained its unique fruit morphology since the Palaeogene. It is also possible that slow morphological evolutionary rates within the genus contributed to the ecological

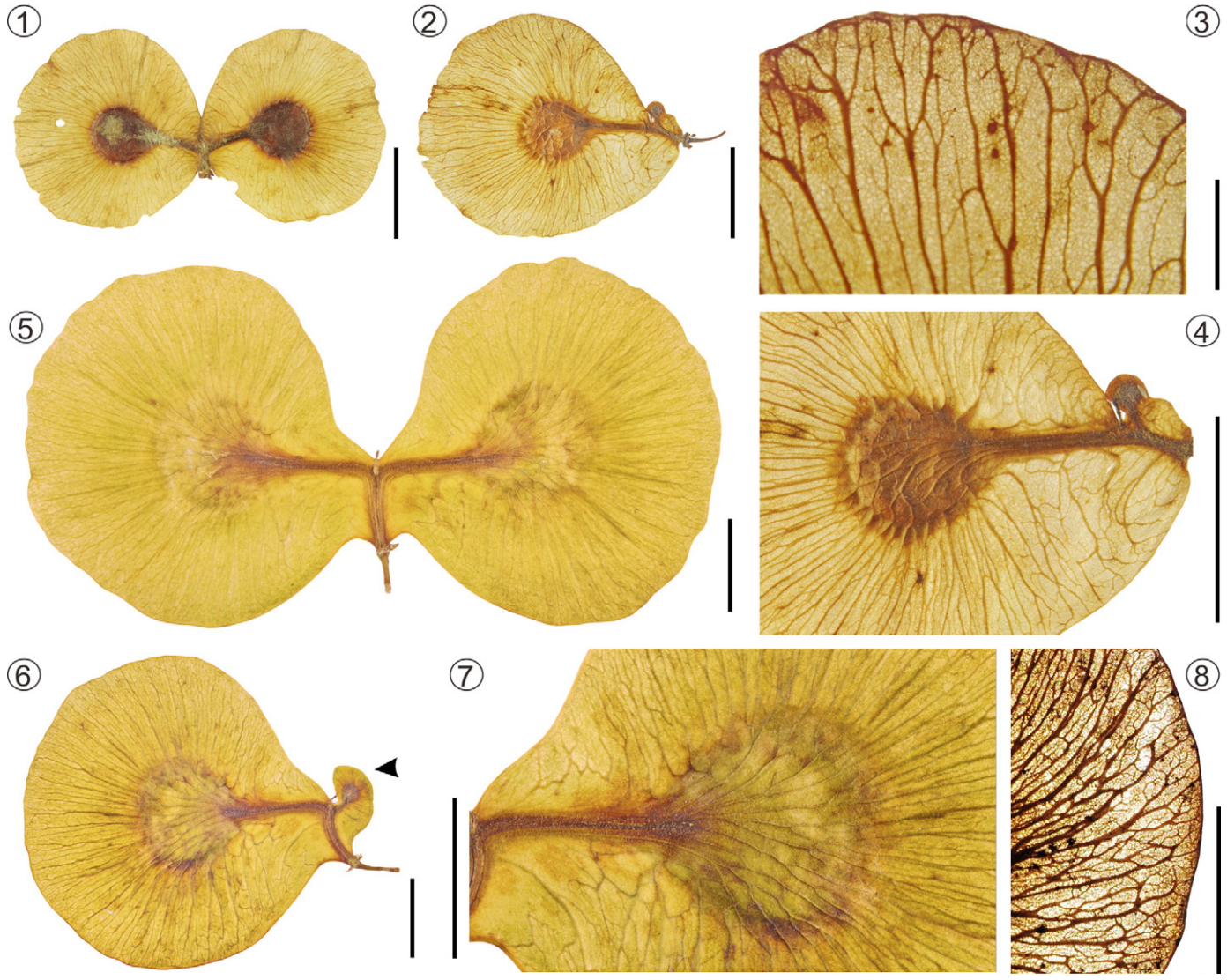

Plate II. Extant winged fruits of *Dipteronia*. 1–4. *Dipteronia sinensis*, fruits from Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN). 1. Typical schizocarp of *D. sinensis* with two fully developed mericarps. Scale bar = 1 cm. 2. Another specimen of *D. sinensis* showing an enlarged mericarp and an undeveloped one (arrow), and remnant perianth at the junction of pedicel with fruits. Scale bar = 1 cm. 3. Details from 2, showing secondary veins over the pericarp and radiating tertiary veins, and reticulum of quaternary veins between the tertiaries. Scale bar = 2 mm. 4. Enlargement from 2, showing the radiating secondary and tertiary veins over the pericarp, the margin of the seed body in the mericarp, and remote secondary and tertiary around the primary veins. Scale bar = 1 cm. 5–8. *Dipteronia dyeriana*, fruits from cultivated individuals in Kunming Institute of Botany, Chinese Academy of Sciences (KUN). 5. Typical schizocarp of *D. dyeriana* with two big fully developed mericarps, and remnant perianth at the junction of pedicel with fruits. Scale bar = 1 cm. 6. Another specimen of *D. dyeriana* showing an enlarged mericarp and an undeveloped one (arrow). Scale bar = 1 cm. 7. Enlargement from 6. Scale bar = 1 cm. 8. Close up of the mericarp, showing the reticulum of the tertiary near the margin of the mericarp. Scale bar = 5 mm.

restriction of the palaeoendemic clades (Jordan et al., 2015). Therefore, the central and southern regions of China, which experienced relative tectonic and climatic stability, provided suitable habitats for these palaeoendemic taxa.

5. Conclusions

We report a new occurrence of the species *Dipteronia brownii* McClain et Manchester from the early Oligocene of Yunnan based on diagnostic winged fruits. Our fossils show combined characteristics of *Dipteronia sinensis* and *Dipteronia dyeriana*, but are more similar to *D. sinensis* in fruit size; the larger size of *D. dyeriana* might have been a derived character because of allopatric segregation (Bai et al., 2015). Overall, the genus has retained striking morphological similarities since the Palaeogene. This new fossil discovery suggests that the palaeoendemic genus *Dipteronia* was widely distributed in North America and Asia during the Palaeogene, and had existed in southwestern China by the Rupelian. *Dipteronia* became endemic to China by the result of regional extinctions in North America and northern Asia during the Cenozoic (Xing et al., 2016), in association with global cooling and seasonal intensification of precipitation in the Northern Hemisphere since the Oligocene (Eldrett et al., 2009; Zanazzi et al., 2007; Xiao et al., 2010; Zhang et al., 2012).

Acknowledgements

We thank the members of the Paleoecology Research Group, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences for the assistance in collecting fossils; Shi-Tao Zhang (Kunming University of Science and Technology) for geological guidance; Ren-Bin Zhu for providing ecological habitat information and pictures about *Dipteronia sinensis*; Christopher David Barratt, Yanis Bouchenak-Khelladi, Steven R. Manchester and an anonymous reviewer who helped to significantly improve this manuscript. Extant winged fruits of *D. sinensis* were obtained with the aid of Lei Jiang and Fei Zhao from Herbarium of the Kunming Institute of Botany, Chinese

Table 1
Known fossil records of *Dipteronia* and their ages and localities.
The table is after McClain and Manchester (2001) with supplementary fossil records.

No.	Age	Region	Locality	Latitude	Longitude	References
1	Late Palaeocene	USA	Hell's Half Acre, Wyoming	43.015	−107.081	McClain and Manchester (2001)
2	Palaeocene	Russia	Tsagayan Formation, Amur region	51.783	130.222	Akhmetiev et al. (2002); Manchester et al. (2009)
3	Middle Eocene	USA	White Cliffs Sr., Oregon	44.738	−120.473	McClain and Manchester (2001)
4	Middle Eocene	USA	West Branch Creek, Oregon	44.591	−120.259	McClain and Manchester (2001)
5	Middle Eocene	USA	Republic, Washington	48.652	−118.739	McClain and Manchester (2001)
6	Middle Eocene	Canada	One Mile Creek, Princeton, British Columbia	49.350	−120.333	McClain and Manchester (2001)
7	Middle Eocene	Canada	McAbee, British Columbia	50.783	−121.133	McClain and Manchester (2001)
8	Middle Eocene	Canada	Joseph Creek, British Columbia	51.467	−120.117	McClain and Manchester (2001)
9	Middle Eocene	Canada	Horsefly, British Columbia	52.339	−121.417	McClain and Manchester (2001)
10	Middle Eocene	Canada	Driftwood Creek, British Columbia	54.825	−127.017	McClain and Manchester (2001)
11	Late Eocene	USA	Florissant, Colorado	38.910	−105.271	Brown (1937)
12	Late Eocene	USA	Ruby river Basin, Montana	45.219	−112.208	Manchester (1999)
13	Late Eocene	USA	Teater Road, Oregon	44.167	−120.248	McClain and Manchester (2001)
14	Late Eocene	USA	Sumner Spring, Oregon	44.419	−121.109	McClain and Manchester (2001)
15	Late Eocene	USA	White Rock Gulch, Oregon	44.703	−120.474	McClain and Manchester (2001)
16	Late Eocene	USA	Whitecap Knoll, Oregon	44.837	−120.418	Manchester (2000)
17	Early Oligocene	USA	Bridge Creek, Oregon (Painted Hills)	44.641	−120.288	Meyer and Manchester (1997); Bestland et al. (1999)
18	Rupelian	China	Lühe Town, Yunnan	25.140	101.380	This study

Academy of Sciences (KUN). This work was supported by the National Natural Science Foundation of China (No. U1502231) to Zhe-Kun Zhou and (No. 41661134049) to Tao Su, the grant for excellent young scientists in CAS (No. QYZDB-SSW-SMC016) to Tao Su, and the Pioneer Hundred Talents Program of the Chinese Academy of Sciences to Yao-Wu Xing.

References

Akhmetiev, M.A., Kezina, T.V., Kodrul, T.M., Manchester, S.R., 2002. Stratigraphy and flora of the Cretaceous–Paleogene boundary layers in the southeast part of the Zeya–Bureya sedimentary basin. In: Akhmetiev, M.A., Doludenko, M.P., Herman, A.B., Ignatiev, I.A. (Eds.), Special Volume Dedicated to the Memory of the Corresponding Member of the USSR Academy of Sciences, Professor Vsevolod Andreevich Vakrameev (to the 90th Anniversary of His Birth). Geological Institute, Russian Academy of Sciences, Moscow, pp. 275–315 (in Russian).

Bai, G.Q., Li, S., Li, W., Li, Z., Yang, J., Zhao, G., 2015. Interspecific differentiation of the endemic plant genus *Dipteronia* Oliv. Acta Botan. Boreali-Occiden. Sin. 35, 1123–1128 (in Chinese).

Bestland, E.A., Hammond, P.E., Blackwell, D.L.S., Kays, M.A., Retallack, G.J., Stimac, J., 1999. Geologic framework of the Clarno Unit, John Day Fossil Beds National Monument, central Oregon. Ore. Geol. 61, 3–19.

Brown, R.W., 1935. Miocene leaves, fruits, and seeds from Idaho, Oregon, and Washington. J. Paleontol. 9, 572–587.

Brown, R.W., 1937. Additions to some fossil floras of the western United States. U. S. Geol. Surv. Prof. Pap. 186-J, 163–206.

Ding, W.N., Kunzmann, L., Su, T., Huang, J., Zhou, Z.K., 2017. A new fossil species of *Cryptomeria* (Cupressaceae) from the Rupelian of the Lühe Basin, Yunnan, East Asia: implications for palaeobiogeography and palaeoecology. Rev. Palaeobot. Palynol. https://doi.org/10.1016/j.revpalbo.2017.09.003.

Eldrett, J.S., Greenwood, D.R., Harding, I.C., Huber, M., 2009. Increased seasonality through the Eocene to Oligocene transition in northern high latitudes. Nature 459, 969–973.

Fang, J., Wang, Z., Tang, Z., 2011. Atlas of Woody Plants in China: Distribution And Climate. Higher Education Press, Beijing, p. 960.

Favre, A., Päckert, M., Pauls, S.U., Jähnig, S.C., Uhl, D., Michalak, I., Muellner-Riehl, A.N., 2015. The role of the uplift of the Qinghai–Tibetan Plateau for the evolution of Tibetan biotas. Biol. Rev. 90, 236–253.

Feng, G., Mao, L., Sandel, B., Swenson, N.G., Svenning, J.C., 2015. High plant endemism in China is partially linked to reduced glacial–interglacial climate change. J. Biogeogr. 43, 145–154.

Ferguson, D.K., Liu, Y.S., Zetter, R., 1997. The paleoendemic plants of East Asia: evidence from the fossil record for changing distribution patterns. In: Jablonski, N.G. (Ed.), The Changing Face of East Asia During the Tertiary and Quaternary. Centre of Asian Studies, The University of Hong Kong, Hong Kong, pp. 359–371.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hsu, J., 1983. Late Cretaceous and Cenozoic vegetation in China, emphasizing their connections with North America. Ann. Mo. Bot. Gard. 490–508.

Huang, J.H., Chen, J.H., Ying, J.S., Ma, K.P., 2011. Features and distribution patterns of Chinese endemic seed plant species. J. Syst. Evol. 49, 81–94.

Huang, J.H., Chen, B., Liu, C.R., Lai, J.S., Zhang, J.L., Ma, K.P., 2012. Identifying hotspots of endemic woody seed plant diversity in China. Divers. Distrib. 18, 673–688.

Huang, Y.J., Jacques, F.M., Su, T., Ferguson, D.K., Tang, H., Chen, W.Y., Zhou, Z.K., 2015. Distribution of Cenozoic plant relicts in China explained by drought in dry season. Sci. Rep. 5, 14212.

Huang, J.H., Huang, J.H., Lu, X.H., Ma, K.P., 2016a. Diversity distribution patterns of Chinese endemic seed plant species and their implications for conservation planning. Sci. Rep. 6, 33913.

Huang, J., Su, T., Lebereton-Anberrée, J., Zhang, S.T., Zhou, Z.K., 2016b. The oldest *Mahonia* (Berberidaceae) fossil from East Asia and its biogeographic implications. J. Plant Res. 129, 209–223.

Ivany, L.C., Patterson, W.P., Lohmann, K.C., 2000. Cooler winters as a possible cause of mass extinctions at the Eocene/Oligocene boundary. Nature 407, 887–890.

Jordan, G.J., Harrison, P.A., Worth, J.R., Williamson, G.J., Kirkpatrick, J.B., 2015. Palaeoendemic plants provide evidence for persistence of open, well-watered vegetation since the Cretaceous. Glob. Ecol. Biogeogr. 25, 127–140.

Kreft, H., Jetz, W., 2013. Comment on "An update of Wallace's zoogeographic regions of the world". Science 341, 343.

Lielke, K., Manchester, S.R., Meyer, H., 2012. Reconstructing the environment of the northern Rocky Mountains during the Eocene/Oligocene transition: constraints from the palaeobotany and geology of south-western Montana, USA. Acta Palaeobot. 52, 317–358.

Linnemann, U., Su, T., Kunzmann, L., Spicer, R.A., Ding, W.N., Spicer, T.E.V., Zieger, J., Hofmann, M., Moraweck, K., Gartner, A., Gerdes, A., Marko, L., Zhang, S.T., Li, S.F., Tang, H., Huang, J., Mulch, A., Mosbrugger, V., Zhou, Z.K., 2018. New U–Pb dates show a Paleogene origin for the modern Asian biodiversity hot spots. Geology https://doi.org/10.1130/G39693.1.

Liu, J., Tian, B., 2007. Origin, evolution, and systematics of Himalaya endemic genera. Newsletter of Himalayan. Botany 40, 20–27.

Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie, R.M., Pearson, A., 2009. Global cooling during the Eocene–Oligocene climate transition. Science 323, 1187–1190.

López-Pujol, J., Zhang, F.M., Sun, H.Q., Ying, T.S., Ge, S., 2011. Centres of plant endemism in China: places for survival or for speciation? J. Biogeogr. 38, 1267–1280.

Lu, H., 2015. Driving force behind global cooling in the Cenozoic: an ongoing mystery. Sci. Bull. 60, 2091–2095.

Ma, Q.W., Li, F.L., Li, C.S., 2005. The coast redwoods (*Sequoia*, Taxodiaceae) from the Eocene of Heilongjiang and the Miocene of Yunnan, China. Rev. Palaeobot. Palynol. 135, 117–129.

Manchester, S.R., 1999. Biogeographical relationships of North American Tertiary floras. Ann. Mo. Bot. Gard. 86, 472–522.

Manchester, S.R., 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County. Oregon. Ore. Geol. 62, 51–63.

Manchester, S.R., Chen, Z.D., Lu, A.M., Uemura, K., 2009. Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. J. Syst. Evol. 47, 1–42.

Manos, P.S., Donoghue, M.J., 2001. Progress in Northern Hemisphere phytogeography: an introduction. Int. J. Plant Sci. 162, S1–S2.

Marincovich, L., Gladenkov, A.Y., 1999. Evidence for an early opening of the Bering Strait. Nature 397, 149–151.

McClain, A.M., Manchester, S.R., 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phytogeographic history of the Aceroideae. Am. J. Bot. 88, 1316–1325.

Meyer, H.W., Manchester, S.R., 1997. The Oligocene Bridge Creek Flora of the John Day Formation. Oregon University of California Press, Berkeley, Los Angeles, London.

Milne, R.I., 2006. Northern hemisphere plant disjunctions: a window on Tertiary land bridges and climate change? Ann. Bot. 98, 465–472.

Milne, R.I., Abbott, R.J., 2002. The origin and evolution of tertiary relict floras. Adv. Bot. Res. 38, 281–314.

Ouyang, Z.Q., Cheng, Q., Zhang, X., Yang, X., Wang, J., 2007. Current Status of Rare *Dipteroina dyeriana* and Countermeasures for Its Protection. vol. 32. Yunnan

Introduction and Propagation Center for Rare and Endangered Plants, pp. 143–146 (in Chinese).
Su, T., Liu, Y.S., Jacques, F.M.B., Huang, Y.J., Xing, Y.W., Zhou, Z.K., 2013. The intensification of the East Asian winter monsoon contributed to the disappearance of *Cedrus* (Pinaceae) in southwestern China. Quat. Res. 80, 316–325.
Sun, J., Ni, X., Bi, S., Wu, W., Ye, J., Meng, J., Windley, B.F., 2014. Synchronous turnover of flora, fauna, and climate at the Eocene–Oligocene boundary in Asia. Sci. Rep. 4, 7463.
Tiffney, B.H., 1985. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J. Arnold Arbor. 66, 73–94.
Tiffney, B.H., Manchester, S.R., 2001. The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. Int. J. Plant Sci. 162, S3–S17.
Weber, W.A., 2003. The Middle Asian element in the southern Rocky Mountain flora of the western United States: a critical biogeographical review. J. Biogeogr. 30, 649–685.
Wen, J., 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. Annu. Rev. Ecol. Syst. 30, 421–455.
Wen, J., 2001. Evolution of eastern Asian–eastern North American biogeographic disjunctions: a few additional issues. Int. J. Plant Sci. 162, S117–S122.
Wen, J., Nie, Z.L., Ickert-Bond, S.M., 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. J. Syst. Evol. 54, 469–490.
Willis, K.J., Niklas, K.J., 2004. The role of Quaternary environmental change in plant macroevolution: the exception or the rule? Philos. Trans. R. Soc. B 359, 159–172.
Wissink, G.K., Hoke, G.D., Garzione, C.N., Jing, L.Z., 2016. Temporal and spatial patterns of sediment routing across the southeast margin of the Tibetan Plateau: insights from detrital zircon. Tectonics 35, 2538–2563.
Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere: data from fossil plants make it possible to reconstruct Tertiary climatic changes, which may be correlated with changes in the inclination of the earth's rotational axis. Am. Sci. 66, 694–703.
Wolfe, J.A., 1980. Tertiary climates and floristic relationships at high latitudes in the northern hemisphere. Palaeogeogr. Palaeoclimatol. Palaeoecol. 30, 313–323.
Wolfe, J.A., Wehr, W., 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. U.S. Geol. Surv. Bull. 1597, 1–25.
Wood, C.E., 1972. Morphology and phytogeography: the classical approach to the study of disjunctions. Ann. Mo. Bot. Gard. 59, 107–124.
Wu, Z., Sun, H., Zhou, Z., Peng, H., Li, D., 2007. Origin and differentiation of endemism in the flora of China. Front. Biol. 2, 125–143.
Xiang, Q.Y., Soltis, D.E., Soltis, P.S., 1998. The eastern Asian and eastern and western North American floristic disjunction: congruent phylogenetic patterns in seven diverse genera. Mol. Phylogenet. Evol. 10, 178–190.
Xiao, G., Abels, H.A., Yao, Z., Dupont-Nivet, G., Hilgen, F.J., 2010. Asian aridification linked to the first step of the Eocene–Oligocene climate transition (EOT) in obliquity-dominated terrestrial records in Xining basin, China. J. Earth Sci. 21, 219–220.
Xing, Y., Ree, R.H., 2017. Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/pnas.1616063114.
Xing, Y., Gandolfo, M.A., Linder, H.P., 2016. The Cenozoic biogeographical evolution of woody angiosperms inferred from fossil distributions. Glob. Ecol. Biogeogr. 24, 1290–1301.
Xu, T., Chen, Y., Jong, P.C.d., Oterdoom, H.J., Chang, C.S., 2008a. Aceraceae. In: Wu, Z.Y., Raven, P.H. (Eds.), Flora of China. vol. 11. Science Press, Beijing, pp. 515–517 Missouri Botanical Garden Press, St. Louis.
Xu, J.X., Ferguson, D.K., Li, C.S., Wang, Y.F., 2008b. Late Miocene vegetation and climate of the Lühe region in Yunnan, southwestern China. Rev. Palaeobot. Palynol. 148, 36–59.
Yi, T.M., Li, C.S., Xu, J.X., 2003. Late Miocene woods of Taxodiaceae from Yunnan, China. Acta Bot. Sin. 45, 384–389.
Zanazzi, A., Kohn, M.J., MacFadden, B.J., Terry, D.O., 2007. Large temperature drop across the Eocene–Oligocene transition in central North America. Nature 445, 639–642.
Zhang, Z.Y., 1996. Multiple Classification and Correlation of the Stratigraphy in China. China University of Geosciences Press, Wuhan.
Zhang, Y.L., Ferguson, D.K., Ablaev, A.G., Wang, Y.F., Li, C.S., Xie, L., 2007. *Equisetum* cf. *pratense* (Equisetaceae) from the Miocene of Yunnan in southwestern China and its paleoecological implications. Int. J. Plant Sci. 168, 351–359.
Zhang, R., Kravchinsky, V.A., Yue, L., 2012. Link between global cooling and mammalian transformation across the Eocene–Oligocene boundary in the continental interior of Asia. Int. J. Earth Sci. 101, 2193–2200.
Zhang, M., Hu, W.B., Yu, Y.M., 2014. The Characteristics of Growing Communities and Protection Strategies of *Acer miaotaiense*, *Dipteronia sinensis*, *Euptelea pleiospermum*, *Tetracentron sinense* in Lengshuiquangou, Xiaolongshan. vol. 30. Gansu Science and Technology, pp. 153–155 (in Chinese).
Zhang, D.C., Ye, J.X., Sun, H., 2016. Quantitative approaches to identify floristic units and centres of species endemism in the Qinghai–Tibetan Plateau, south-western China. J. Biogeogr. 43, 2465–2476.
Zhou, Z.K., 2013. Origin and development of the Chinese flora. In: Blackmore, S., Hong, D.Y. (Eds.), Plants of China: A Companion to the Flora of China. Science Press, Beijing, pp. 95–96.
Zhou, Z.K., Momohara, A., 2005. Fossil history of some endemic seed plants of East Asia and its phytogeographical significance. Acta Bot. Yunnanica 27, 449–470 (in Chinese).